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Dispersion of Spores of Fungi by Insects as in Phalloidei.

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Fig. 1.

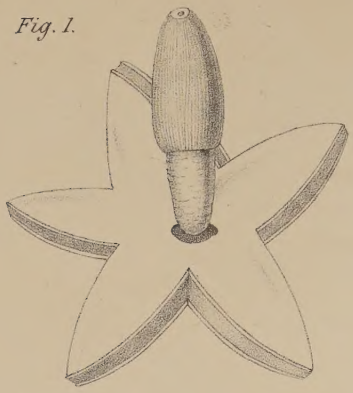
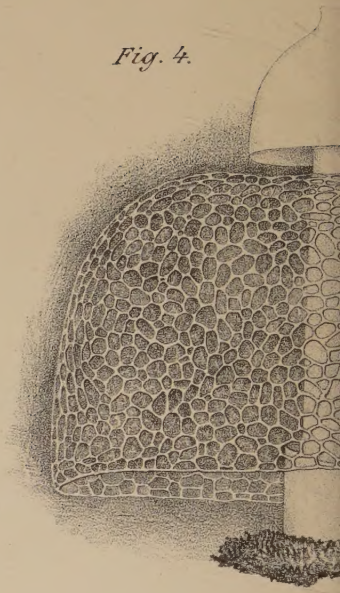


Fig. 2.

Fig. 4.



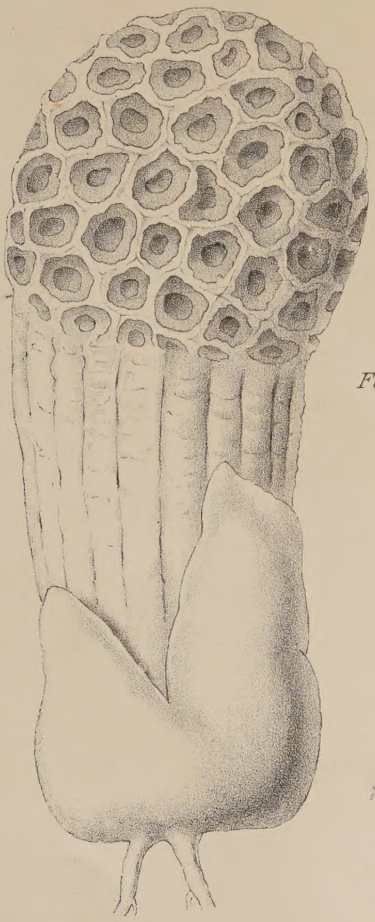


Fig. 3.

Fig. 6.

Fig. 7.

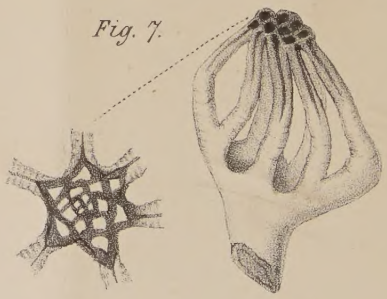


Fig. 5 a.

Fig. 5.

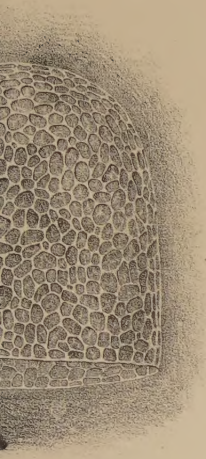
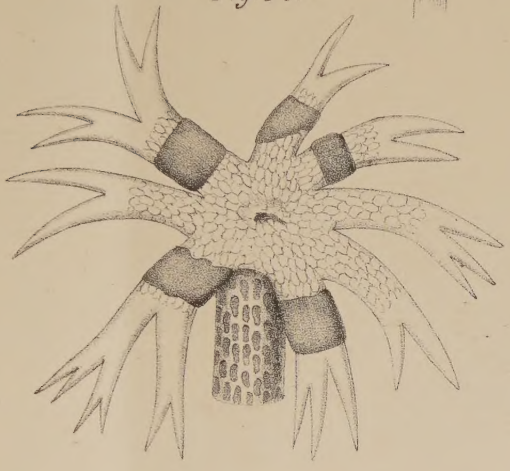


Fig. 5 b.



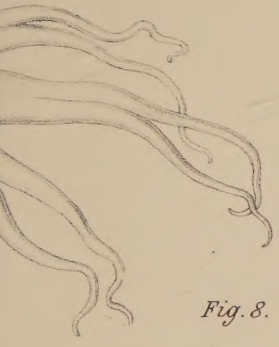
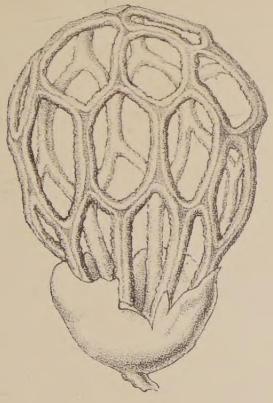


Fig. 9.

Fig. 8.



University Press, Oxford

Description p. 238

The Dispersion of the Spores of Fungi by the Agency of Insects, with special reference to the Phalloidei.

BY

T. WEMYSS FULTON, M.B.

With Plate XV.

1. Introductory.

IT may be desirable to explain that this investigation originated while I was engaged in the study of the adaptations of flowers for insect visits, and purely from a consideration of the possible function of the strong odour emitted by *Phallus impudicus*. It was only on the completion of my paper that I discovered that Professor Ráthay and Dr. Haas[1] had previously worked at the subject. The first notice of the probable adaptation of *Phallus* for the attraction of insects seemingly appeared anonymously in *Science Gossip*[2], and a fuller account by 'W. R. G.' in the *Bulletin of the Torrey Botanical Club* in the following year[3]. But these notices were more in the way of surmise than as showing the results of systematic investigation. The paper referred to by Messrs. Ráthay and Haas embodies the results of observation and of chemical analysis of the sporiferous hymenial slime, and indicates the adaptation of *Phallus* and its congeners for insect visitation. In the following paper the research is carried

[1] Sitzungsb. d. Mathem.-Naturwiss. Akad. d. Wissenschaft., Bd. lxxxvii, Heft 1, p. 18. Wien, 1883.

[2] November 1879.

[3] Vol. vii, p. 30, 1880.

[Annals of Botany, Vol. III. No. X. May 1889.]

further, inasmuch as the spores were successfully germinated, and a comparative analysis of the physical properties of the *Phalloidei* is given.

2. Phallus Impudicus.

In the case of Cryptogams the dispersal of the spores usually takes place in a purely fortuitous manner, multitudes being blown about by the wind or carried by the movement of water. But among some of the higher and most complex fungi there exist contrivances and adaptations as remarkable and advantageous as among the Phanerogams, by which the more definite and purposive actions of insects are utilised for the dissemination of the spores.

I have been able to investigate the subject completely only in the case of one fungus, *Phallus impudicus*, the common 'Stinkhorn' of our woods; but the conclusions will be found to apply to many others.

The histology and development of *Phallus* have been described by Berkeley[1], Corda[2], Lespiault[3], Rossmann[4], and especially De Bary[5], and several members of the group more recently by Fischer[6]; but to understand the adaptations for the dispersion of the spores it will be necessary to give a brief account of its structure and life-history.

Phallus is chiefly found in woods, but may also occur elsewhere—as in gardens, fields, etc.

The hymenophore or reproductive portion consists in its earliest stages of minute swellings, which arise on the underground mycelium. These at first are homogeneous, but gradual differentiation goes on, so that towards maturity the following parts may be recognised: (1) An enclosing cortical portion, the volva or peridium, composed of three layers; (*a*) an outer

[1] Ann. Nat. Hist., vol. iv, p. 158, Pl. V, 1840.
[2] Icones Fungorum, Tom. v, p. 71, Taf. VII, 1842.
[3] Ann. d. Sci. Nat., Sér. 5, Tom. iv, p. 44, Pl. I, 1845.
[4] Bot. Zeit., 1853, p. 185, Taf. IV.
[5] Vergleich. Morphol. u. Biol. der Pilze, p. 346, 1884.
[6] Ann. du Jardin botanique de Buitenzorg, vol. vi, part 1, p. 1, Pls. I–V, 1886.

firm skin or membrane, the external peridium; (*b*) an inner thin membrane, the internal peridium; (*c*) an intermediate much thicker layer of translucent, pale yellowish-brown gelatinous material, the gelatinous layer. At the base there is a cup-shaped portion which supports the stem, and is continuous laterally by its margin with the peridial layers, and below with the mycelium. (2) A central medullary portion, composed of two very different structures: (*a*) the gleba, or spore-bearing part, which forms a hollow conical cap, lying within the inner peridium and surrounding the upper portion of the stem, to the apex of which it is firmly attached. Its outer surface bears the hymenium, and is honeycombed by a large number of irregular chambers or depressions, in which the mass of spores is lodged. (*b*) The stem, consisting of a cylinder whose walls at this stage are firm and solid-looking, and composed of a multitude of small, vertically compressed cavities filled with jelly.

The volva is at first concealed beneath the surface of the soil, but towards maturity it breaks through the ground, and the exposed part gradually becomes conical and finally ruptures, the stem rapidly lengthening and elevating the gleba in the air. These phenomena depend upon a peculiar mechanical change which occurs in the stem. The gelatinous contents of the flattened cavities disappear, and they become excessively dilated, the previously compact stem increasing threefold or fourfold in magnitude and becoming open and spongy, the distension of the cavities being due to the secretion of air[1]. The protrusion and elevation of the gleba take place with great rapidity, and may be completed in from half-an-hour to two or three hours, the gleba attaining a height of from 5 or 6 to 8 or 10 inches above the surface of the ground. The utility of this sudden elevation by the substitution of a rapid mechanical process for the slower process of simple growth will be evident in the sequel.

At the time of emergence, and for a brief interval afterwards,

[1] De Bary, op. cit. p. 348. It struck me as being purely mechanical, like the expansion of a compressed sponge, air finding its way in by ruptures of the walls.

the hymenial surface is firm and solid, greenish-grey in colour, and emits a faint, mawkish, but sweetish and honey-like odour[1], which is attractive to house-flies (*Musca domestica*). Very soon, however, and before the elongation of the stem is completed, it begins to darken, the odour becomes somewhat foetid, and the consistency changes, so that it gets rather sticky and tenacious. A little later it is dark green, almost black, the odour is very strong and repulsively foetid, and its consistency slimy or almost fluid. These changes in the physical character of the hymenial mass begin at the apex of the gleba, and rapidly extend downwards. They seem to depend largely upon the influence of light, for if one side be protected from its action the change in consistency and colour is retarded on that side. A specimen I kept in a darkened place only very partially liquefied and did not drop off, but dried up into a hard, black, shining, odourless mass. When examined microscopically the foetid fluid is seen to contain myriads of spores, each 0·03 mm. long. The rupture of the peridium and the changes I have described occur during the hot months of the year, from the early part of July till the end of September, and therefore at a time when insect life is very abundant, and when myriads of flies abound. As soon as the stercoraceous odour is developed, the liquefying hymenium is visited by large numbers of flies, which sometimes, on hot sunny days, almost cover it, and suck up the fluid mass with great avidity, very soon removing the most of it. When the weather is dull and cloudy or cold fewer flies are to be seen on the glebae; but it is possible that the deliquescence then goes on more slowly.

The fact that flies are attracted to the stinking slime of *Phallus impudicus* has been long known to botanists. The earliest notice I have found of this circumstance occurs in some Latin verses[2] composed by the old botanist Hadrianus

[1] It has been shown by Messrs. Ráthay and Haas (op. cit. p. 43) that the liquefying hymenium contains three forms of sugar, laevulose, dextrose, and another, intermediate between dextrose and gum.

[2] Quoted by von Schlechtendal, Linnaea, Bd. xxxi, p. 147, 1862.

Junius, who died in 1575, but whose verses were not published until 1616. It is as follows:—

'Vertice supremo praefert exile foramen
Quod stipant avide muscarum examina nigra.'

Jacob Christian Schäffer, in 1760, described the attractiveness of *Phallus* for flies[1]. Ventenat[2], writing at the end of last century, says it diffuses 'une odeur infecte, qui attire une foule d'insectes'; and Greville[3] remarks: 'So very offensive is the smell of this substance that it is seldom allowed to drop away according to the course of nature, but is generally consumed in a few hours by flesh flies.' Berkeley[4] also says: 'The dripping hymenium affords a welcome food to multitudes of flies.'

The liquefaction of the hymenium has been generally regarded (e.g. by De Bary) as a means of allowing the spores to drop off in the fluid; but this would tend to localise rather than to scatter them. Von Schlechtendal and Dr. Cooke, however, recognised the relation of the liquefaction to insects' visits. The former says[5]:—'Dann beginnt das Hymenium und vielleicht auch die nahe gelegenen Theile zu zerfliessen, um die Sporen mit der dabei entstehenden übelriechenden Flüssigkeit zur Aussaat zu bringen, was zum Theil auch dadurch zu geschehen scheint, dass die Thierwelt, indem sie diesen sporenhaltenden Saft oder die Pilze selbst verzehrt, für deren weitere Verbreitung Sorge trägt.' Dr. Cooke[6] also surmised the value of the insects' visits when he says: 'This gelatinous substance has nevertheless a peculiar attraction for insects, and it is not altogether romantic to believe that in sucking up the fetid slime they also imbibe the spores, and transfer them from place to place, so that even amongst fungi insects aid in the dissemination of species.'

[1] Der Gichtschwamm mit grünschleimigem Hute, p. 13, 1760.
[2] Mém. de l'Instit. Nation. d. Sci. Art., Tom. i, p. 519, 1798.
[3] Scot. Crypt. Flora, vol. iv, tab. 213, 1826.
[4] Introd. Crypt. Bot., p. 347, 1857.
[5] Linnaea, Bd. xxxi, p. 115, 1862.
[6] Fungi: their Nature, Influence, and Uses, p. 123, 1875.

In regard to the insects which visit the foetid slime, I observed two species of flies ; (1) the ordinary blue-bottle (*Musca vomitoria*), which was very abundant, and (2) a large bright metallic green fly (*Musca Caesar*). On partially empty glebae which had fallen to the ground I found several small brown beetles and small dung-flies. Prof. Ráthay gives a list of fourteen species observed by him, most of which visit both dung and nectariferous flowers. It is probable that further observation will show that *Phallus* is visited by a large number of the numerous insects which visit putrid substances ; for it is evident that we have here to deal with a case of mimicry, in which such substances are successfully imitated. This is shown not merely by the physical properties of the deliquescing hymenium and the action of the flies, but also by the fact that these insects sometimes deposit their eggs on the external peridium of the burst volva, or on the ground in its immediate neighbourhood. In the majority of cases this is doubtless an instance of an instinct at fault, for I have not found a volva, *in situ*, attacked by the maggots, which probably soon perish. In one case, however, where the unruptured volva had lost its vitality while I was experimenting with it and lay loose on the surface of the soil, I found it riddled by a number of maggots which had thriven on their dietary. They were of two kinds, the ordinary maggot of the blow-fly, and one of about the same length but brown, flattened, and with lateral bristles.

Having observed the action of the flies in sucking up the spore-containing slime, the questions were naturally suggested : (1) What effect has the imbibed matter on the fly? and (2) What effect has the fly on the spores?

In order to determine these points I removed a number of nearly ripe specimens in their native earth, and placed them in town, where they could be more continuously under observation. When the characteristic odour had become developed large numbers of blow-flies rapidly made their appearance and settled on the deliquescing mass. About twenty flies were placed in a box covered with gauze, and supplied from time to time with fresh glebae.

Regarding the first question, the action on the fly, there was no deleterious effect. They lived for about three weeks on this food and then died, and as was to be expected no subsequent change occurred in their bodies.

With respect to the second question, the effect on the spores, it was found in the first place, by microscopical examination, that thousands of spores clung to the feet and proboscides of the flies. These would obviously retain their vitality. The excrements of the flies which soon covered the inside of the box, at first consisted chiefly and then exclusively of spores, microscopically indistinguishable from those directly removed from the gleba.

It was thus clear that the flies transported the spores, but the question was still to be decided whether the spores retained their vitality after passing through the digestive system of the insect, or whether, on the other hand, it was destroyed.

On *a priori* grounds this question would be answered in the affirmative. The rapid mimetic changes in the hymenium, the luring of large numbers of flies, and the fact that the flies carry off the great majority of the spores which they subsequently deposit, all point to adaptation; and to suppose that the vitality of the spores was destroyed would be to assume that a species might with impunity offer facilities for its own extinction. To experimentally determine the point, I adopted the following method for the germination of the spores. A quantity of earth taken from the place where the fungus grew was sterilised by prolonged boiling, and two series of open glass tubes were filled with this and with certain substances as shown in Table I. One tube in each series contained the same material, and to all those of *one* series was added the sporiferous deposit of the flies. Thus each experiment was duplicated, the only factor of difference being that in one series (A) the flies' excrements were present, and in the other series (B) absent. The tubes were then closed with cotton-wool and buried vertically, eight inches apart, in the locality were *Phallus impudicus* grew, near the surface but quite covered with the soil. This was done in September, and in the follow-

ing November it was found that in tubes 3 and 4 of series A a mycelium had sprouted, but not in any of the others. In December tube 3 was found lying empty on the surface, apparently thrown out by the burrowings of a mole, and its contents washed out by rain. In tube 4, however, the snowy white mycelium had increased in extent, ramification, and

TABLE I.

Contents of Tube.	Series A.		Series B.	
	With Flies' Excrements.	Result.	Without Flies' Excrements.	Result.
(*a*)	,, ,, only	No mycelium		
(*b*) Dead flies'		Do.		
1. Chopped beef	,, ,, ,,	Do.[1]	1′ ,, ,,	No mycelium[1]
2. Decaying leaves	,, ,, ,,	Do.	2′ ,, ,,	Do.
3. Rabbits' dung	,, ,, ,,	Mycelium	3′ ,, ,,	Do.
4. Faecal matter	,, ,, ,,	Do.	4′ ,, ,,	Do.

thickness[1]. Unfortunately, on re-examination in the following spring it was found to have died, and was dry, shrunk, and stained yellow. The crowning proof—the development of the hymenophore—is therefore wanting, but as the mycelium had exactly the appearance of that growing naturally and undoubtedly belonging to *Phallus impudicus*, and since it did not appear in the corresponding tubes of series B, exposed to precisely the same influences, but devoid of the sporiferous deposit of the flies, it can scarcely be doubted that it was the product of the spores contained in the latter substance, and that therefore their passage through the digestive canal of the insects does not interfere with their vitality[2].

[1] In tubes 1 and 1′ a fine mould had developed, but not apparently in 4 and 4′.

[2] The mycelium developed in the above experiment was evidently formed by a combination of hyphae from many spores. It does not appear to have been pointed out that the origination of a new individual by the union of the products of spores derived from different individuals of the same species, serves among Cryptogams the same function as cross-fertilisation does among higher organisms. In both cases the new organism is generally the joint product of more than one individual.

We thus see that insects are normally the disseminators of the spores of *Phallus impudicus*, and this fact serves to explain not only the peculiar liquefaction of the hymenium, but many other points in its structure, and furnishes, indeed, the clue to the curious and often *bizarre* forms of other phalloids, which have so often puzzled botanists to explain.

3. The Coprini.

It seems very probable that most or all of those fungi whose spores are ultimately contained in a slimy or liquid substance of dark colour, especially if of foetid odour, and which is freely accessible, will be found to have their spores largely transported by the agency of insects.

We find, for instance, in the genus *Coprinus* many examples fulfilling these conditions. There are between thirty and forty British species of *Coprini*[1], and a brief consideration of their leading characters will not be without interest. The hymenophore, which may vary in height from about half an inch to six or seven inches, is often very delicate and fugacious, and may in some cases go through all its stages and disappear within twenty-four hours or less. The stem is almost invariably white, and the external surface of the pileus is usually whitish, slate-coloured or brown, sometimes with a reddish tinge, and generally darkens in association with the change in colour of the gills, which in the majority of cases are at first white or pale or pinkish, but ultimately become almost or quite black. In some cases the pileus is conspicuous by its colouring, as in *Coprinus picaceus*, in which the outer surface is pied with white patches on a dark ground. The great character, however, of the *Coprini* is that the hymenial surface deliquesces, the spores becoming immersed in an inky-black fluid, often exceedingly foetid[2]. As is the rule in the Agaricini, the hymenium is in-

[1] Cooke, Handbook Brit. Fung. vol. i, p. 160, et seq. 1871; Illustrations Brit. Fung. Nos. xlii–xliv. Pls. 658–687, 1886.

[2] Dr. Haas found glucose in the deliquescing fluid of some species of *Coprini*. Op. cit. p. 43.

ferior and therefore not so freely exposed as in *Phallus impudicus*, but it is interesting to note that the marginal zone of the pileus generally becomes radially cleft and split up in a stellate manner, the rays thus formed usually curling up so that the hymenial surface is freely exposed, and the whole pileus may resemble an umbrella turned inside out (Pl. XV, Fig. 9). In *Coprinus fimentarius* the revolute pileus may droop, flower-like, owing to flaccidity of the portion of the stem just below it[1]. In some cases, from the radial fissuring and the curling up of the pileus, combined with peculiarities of colouring, a curious superficial resemblance to the flowers of some Compositae may be recognised, the unchanged, often brownish centre representing the disc and the radiate marginal part the rays. Such may be seen in *C. oblectus*, *C. fimetarius*, var. *pullatus*, *C. aratus*, *C. papillatus*, *C. Hendersonii*, *C. narcoticus*, *C. nycthemerus*, *C. radiatus*, and *C. spraguei*[2]. This partial mimicry may possibly be accidental and without advantage, but it is worth noting that the great majority of those species which are markedly revolute, or what I may call flower-like, grow on dung, where flies are abundant, while of those which possess neither of these characters well marked the majority do not grow on dung as a rule. We find further that in many Compositae flies form a large proportion of the floral visitors: in the ox-eye daisy (*Chrysanthemum Leucanthemum*) 36 per cent.[3]; in the daisy (*Bellis perennis*) 48 per cent.[4]; in the wild Chamomile (*Matricaria Chamomila*), which has a strong odour, 65 per cent.[5]; and in each case some of the flies habitually affect putrid substances also. Considering all these facts in relation to the *Coprini*, the assumption is certainly warranted that they exhibit adaptations for the purpose of having their spores transported by insects.

[1] Cooke, op. cit. Pl. 669.
[2] Op. cit. Pls. 661, 669, 675, 676, 680, 682, 683.
[3] Müller's Fertilisation of Flowers (Eng. Transl.), p. 331, 1883.
[4] Op. cit. p. 321.
[5] Op. cit. p. 332.

4. The Phalloidei Generally.

It is however in the Phalloidei, the group to which *Phallus* belongs, that we find the most striking and curious instances of deviation and modification for the purpose of adapting them for the attraction of insects. Their chief and central character, from the point of view of function, is the production, as in *Coprinus*, of a dark, usually foetid fluid, which contains the spores; but this leading feature is supplemented and aided by the development of a receptacle, remarkable and very various in shape, colour, and structure.

The Phalloidei are pre-eminently an order belonging to warm countries, the greater number of the species being confined to tropical or subtropical regions, where of course insect life is most abundant. Although they are widely distributed in these regions (*vide* Table II), we have only four species in Britain, and only one that is at all common, namely *Phallus impudicus*.

They are characterised by the development of the hymenium within a complete volva, usually subterranean and possessing an intermediate gelatinous layer[1]. When the spores are mature and ready for dispersion the volva is ruptured by the rapid mechanical expansion of the receptacle, and the hymenium deliquesces, darkens, and generally becomes foetid. The phenomena connected with the exposure and liquefaction of the hymenium are usually very rapid.

If we consider the character of the receptacle after its escape from the volva we find that it presents considerable variety of

[1] To this glutinous layer, which appears at an early stage, before the formation of the hymenium, various functions have been assigned. It is often regarded as serving to support the expanded receptacle by clasping it after the rupture of the peridium. But it is probable that it may have a protective or defensive function against the attacks of insects; for while many or most of the Agarici and other Hymenomycetes in the wood where *Phallus* grows are ravaged by insects or slugs, I have not found an example of the volva of the latter being attacked, although the stem after its emergence is sometimes eaten by slugs. That the interior is nutritious is shown by the case above cited, in which the maggots no doubt made their way in by the base, where the gelatinous layer is absent, and which is normally always concealed underground.

form, but that the same result of freely exposing the sporiferous slime is attained in each case.

We may divide the different species into two great types for our present purpose.

I. Stalked forms, in which the deliquescing hymenium is superior.

II. Latticed forms, in which the hymenium is contained within a sessile lattice or meshwork.

The first group may be subdivided into three subsidiary ones; (*a*) those with a simple stalk; (*b*) those with a velum, or reticulated expansion surrounding the stem; (*c*) those with the upper portion of the receptacle divided into rays and more or less expanded.

There are several forms which show points of transition. The latticed forms may have a rudimentary stalk (e.g. *Colus*), or the stalked forms a sort of lattice on the pileus (some species of *Simblum, Foetidaria*), etc.

I have given below in Table II a list of all the species of the order of which I have been able to find descriptions or figures, tabulating the colour of the receptacle, external peridium, and sporiferous slime, the odour, the habitat, and the approximate dimensions. In many cases data are wanting; but it must not be assumed that where no odour is stated the species necessarily had none, for many have been described from dried specimens preserved in spirits, and in some cases systematists have apparently not thought it worth while to give all the particulars.

TABLE II.

I. Stalked Forms.

A. *Without Veil or Rays.*

Species.	Colour.			Odour.	Habitat.	Approximate Height in Millimetres.
	Receptacle.	External Peridium.	Deliquescing Hymenium.			
1.[1] *Phallus impudicus*, Lin.	Snowy white[2]	White	Blackish green	Very foetid	Usually bare ground, woods, gardens, &c. Europe	230
2. *Phallus iosmos*, Berk.	Pale reddish grey	Yellowish white	?	?[3]	Sandhills, Lowestoft	120
3. *Phallus Novae-Hollandiae*, Corda	White	White	Blackish green	?	New South Wales	140
4. *Phallus curtus*, Berk.	Dirty white	Yellowish white	Olive-green	Extremely foetid	On the ground, Australia	25
5. *Phallus campanulatus*, Berk.	Dirty white	?	Greenish black	'Scarcely offensive'	On sand-dunes, Uraguay	140
6. *Phallus rubicundus*, Bosc.	Red	Grey	Brown	Foetid	Carolina	175
7. *Phallus xylogenus*, Mont.	White	Blackish	? Blackish	?	On rotten wood, Cayenne	12
8. *Phallus canariensis*, Mont.	Rose-red	Rose-red	?	?	On the ground, Canary Islands	95
9. *Phallus roseus*, Delile.	Reddish	?	Dark	?	Egypt	
10. *Phallus Watsoni*, Berk.	Pileus red	?	?	?	Australia	75
11. *Ithyphallus* (*Phallus*) *tenuis*, Fischer.	Bright creamy yellow.	?	Olive green	No odour	Fallen trunks, Java.	100
12. *Phallus* sp.	Deep red	?	?	?	Ceylon	

[1] The figures refer to the Bibliography, p. 235. [2] Red varieties have been described.

[3] Curtis, who discovered and first figured this species, says it 'had a scent somewhat like violets at a distance, when growing, but was very offensive when dried'; but, as Berkeley remarks, this is so much opposed to the general rule that it stand in needs of confirmation.

A. *Without Veil or Rays* (continued).

Species.	Colour.			Odour.	Habitat.	Approximate Height in Millimetres.
	Receptacle.	External Peridium.	Deliquescing Hymenium.			
13. *Cynophallus caninus*, Fries	White, orange or pinkish; pileus red	Brownish white	Olive-green	Foetid	Amongst decayed leaves in woods, Europe	
14. *Cynophallus bambusinus*, Zöll.	Stem rose red; pileus deep purple red	White	?	?	On bamboo trunks, Java	150
15. *Dictyophallus aurantiacus*, Mont.	Orange	White	? Dark orange red (Corda)	Foetid	Bare ground, Pondicherry	90
16. *Staurophallus Senegalensis*, Mont.	White	White	?	?	On rotten wood, Senegal	240
17. *Aserophallus cruciatus*, Lepr. et Mont.	White	White	Dark olive	?	On rotten wood, Cayenne	20
18. *Simblum peri-phragmoides*, Klotsch	Yellowish	White	Dark green	Foetid	On the ground, Mauritius	90
19. *Simblum gracile*, Berk.	Pale yellow	?	Blackish	?	On the ground in open places, Ceylon	90
20. *Simblum sphaerocephalum*, Schlecht.	Brick-red	White	Dark violet	'Horribly foetid'	On the ground in woods, South America	100
21. *Simblum flavescens*, Kurtz	Yellow	?	Olive	?	On bamboo trunks, Java	150
22. *Foetidaria Coccinea*, Aug. St. Hil.	Scarlet	White	?	Extremely foetid	Cultivated places, Brazil	140
23. '*Phallus impudicus*,' Loureiro [1]	White; cap or ? velum reddish	?	?	Foetid	By hedges, Cochin China	
24. '*Clathrus campana*,' Loureiro [1]	White	White	?	Foetid	Gardens, Cochin China	125

[1] These two species have doubtful affinities (see von Schlechtendal, Linnaea, Bd. xxxi, p. 194).

B. *With Veil.*

Species.	Colour.			Odour.	Habitat.	Approximate Dimensions in Millimetres.	
	Receptacle.	External Peridium.	Deliquescing Hymenium.			Height.	Breadth of Veil.
25. *Dictyophora indusiatus*, Ventenat	White; veil becomes reddish	?	?	Not foetid	Surinam, Cayenne	150	38
26. *Dictyophora brasiliensis*, Schlecht.	White	?	Dark olive	?	Brazil	150	75
27. *Dictyophora Daemonum*, Rumph.	White or delicate yellow	Grey	?	Foetid	India, Ceylon, Java		
28. *Dictyophora speciosa*, Klotsch	White	?	?	?	On the ground, Luzon, Philippines	140	145
29. *Dictyophora tahitiensis*, Schlecht.	White	?	?	?	Tahiti	140	75(?)
30. *Dictyophora radicatus*, Mont.	'Totus fuliginosus'	Pinkish brown	Olive-green	?	On the ground, Cayenne	100	60
31. *Dictyophora duplicatus*, Bosc.	White; pileus yellow	Greyish	?	Very foetid	Carolina		
32. *Dictyophora tunicatus*, Turp.	White	Whitish	Dark green	?	? Domingo, Guiana, Angola	150	80
33. *Dictyophora subuculatus*, Mont.	Whitish	Whitish	Olive then black	Foetid	Algiers	100	
34. *Dictyophora merulina*, Berk.	Brick red	?	?	?	Java		
35. *Dictyophora phalloidea*, Lév.	White	Brownish	?	?	On the ground in woods, Java, Cuba	150	65
36. *Dictyophora campanulata*, Nees.	White	White	Brownish greeen	?	On the ground Java.	150	?

C. *With Rays.*

Species.	Colour.			Odour.	Habitat.	Approximate Dimensions in Millimetres.	
	Receptacle.	External Peridium.	Deliquescing Hymenium.			Height.	Breadth.
37. *Lysurus Mokusin*, Cibot	Stem pink; rays intense red	White	Green	Very foetid	On rotten mulberry leaves, China	75	
38. *Lysurus aseroëformis*, Corda	Stem white; rays red above, yellowish white below	White	Dark olive-green	?	Australia	140	75
39. *Lysurus Gardneri*, Berk.	White	White	Dark brown	?	On the ground, Ceylon	150	
40. *Lysurus corallocephalus*, Welw. & Curr.	Stem white; rays scarlet	Whitish	?	Foetid	Sandy, clayey soil, Angola	125	65
41. *Aseroë actinobola*, Corda	Stem pink; lower surface of rays yellow, upper surface scarlet	White	Dark brown	?	On rotten wood, Sydney	50	100
42. *Aseroë viridis*, Berk.	metallic green; or red	Whitish	?	?	Clay banks, New Zealand	25	65
43. *Aseroë rubra*, Labill.	Stem reddish; rays pale red	White	'Green'	?	Among moss and rubbish, Australia, Tasmania	60	50
44. *Aseroë pentactina*, Endlicher	Rays pale red	White	'Green'	?	Australia	60	85
45. *Aseroë Zeylanica*, Berk.	Stem pink; rays bright scarlet	Purple	'Bright purple'	?	On the ground in woods, Ceylon	50	140
46. *Aseroë Junghuhnii*, Schlecht.	Rays red	White	Blackish	?	In woods, Java	65	250
47. *Calathiscus sepia*, Mont.	Pale rose	White	Blackish	Foetid	On the ground in woods, Hindostan	114	65

II. Latticed Forms.

Species.	Colour.			Odour.	Habitat.	Approximate Dimensions in Millimetres.	
	Receptacle.	External Peridium.	Deliquescing Hymenium.			Height.	Breadth.
48. *Laternea triscapa*, Turpin	Pale vermilion; white below	White	?	?	St. Domingo. In sandy pine woods, Cuba, Chili	50	30
49. *Laternea columnata*, Bosc.	Scarlet	?	?	Very foetid	Carolina	75	
50. *Laternea pusilla*, Berk. & Curt.	Scarlet above, white below	White	?	?	On the ground, Cuba	25	
51. *Laternea angolensis*, Welw. & Curr.	Snowy white	Dusky	Black	Not foetid	Sandy soil, Angola	125	50
52. *Colus hirudinosus*, Cav. et Séch.	White below, deep orange red above	White	Dark olive	Not foetid	Amongst moss and lichens, Toulon	30	85
53. *Clathrus cancellatus*, Linn.	Scarlet[1]	White	Olive, brown, or blackish	Very foetid	On the ground in woods, &c., Europe, India, Algiers, New Zealand	110	20
54. *Clathrus pusillus*, Berk.	Bright ruby red; paler below	White	Dark green	?	On the ground, Australia	50	30
55. *Clathrus crispus*, Turpin	Orange and scarlet	White	Purple	?	On the ground and among grass, Australia, Cayenne. On rotten wood, St. Domingo, Cuba	90	85
56. *Clathrus crispus*, var. β *obovatus*, Berk.	'Salmon-coloured'[2]	White	'Brownish-green internally'	Odourless	Sand-dunes, Uruguay	75	50
57. *Clathrus delicatus*, Berk. & Broome	'Pale'	Brown	?	?	On rotten trees, Ceylon	12	
58. *Ileodictyon cibarium*, Tulasne	White	White	Blackish	'Sub-inodorous'	Meadows & woods, New Zealand		
59. *Ileodictyon gracile*, Berk.	White	White	Olive-green	?	On the ground, Australia	55	50

[1] In exceptional cases the colour of *Clathrus cancellatus* varies through orange to yellow, or through pink to white. Some enormous specimens have been described, as large as 49 by 47 centimetres (Bull. Soc. Bot. de France, Tom. xx, p. 132, 1873).

[2] Apparently described from specimens still enclosed within the peridium.

In the first group, the simple stalked forms, the deliquescing hymenium is exposed on the upper outer surface of the more or less conical or subglobose pileus (Pl. XV, Figs. 1, 2). The total height varies from scarcely half an inch to nearly or quite a foot. The colour of the receptacle is red or reddish in 45·8 per cent., white or whitish in 37·5 per cent., and yellowish in 16·6 per cent. The colour of the external peridium is given in 16 cases: in 11 (68·7 per cent.) it is white or whitish, in two yellowish white, the other three being reddish, blackish, and brownish respectively. The colour of the hymenium is given in 15 cases, and it is dark in all except *Dictyophallus aurantiacus*. The statement that the hymenium in this species is orange-red is not made by Montagne, who first described it, but by Corda[1]. It is probably a mistake, for Corda had only a dried specimen, and very likely one with a naked pileus for examination; and as the pileus itself is deep orange-red (as in *Cynophallus caninus*, where the hymenial substance is olive-green), it is probable that when Corda moistened or scraped a portion of it to examine the spores the colouring matter was communicated to the substance removed. The odour is given in 12 cases: in 11 it is more or less foetid, and in one not foetid.

In the second group the receptacle has essentially the same form as in the first, but there is the addition of a remarkable reticulated expansion attached below the pileus, usually campanulate in form and spreading out around the stem like a frill or crinoline. It may be relatively small or close to the stem, as in *Dictyophora tahitiensis*, Schlecht. (*Phallus Daemonum* of Hooker) and *Dictyophora indusiatus* (Vent.); or it may form a large network reaching nearly to the ground, as in *Dictyophora speciosa*, Klotsch, where it has a circumference of about 20 inches (Pl. XV, Fig. 4). Of the 12 species given in Table II, the receptacle in ten is white, in one brick red, and in one apparently dark. The colour of the external peridium is given in only seven cases; in five it is whitish, and in two brownish. Where described the hymenium is dark. In only four species is the odour given; in three it is foetid, and in one it is not foetid.

[1] Icon. Fung., Tom. vi, p. 19.

The third group comprises some forms very remarkable in shape and colouration. The superior margin of the receptacle is divided into erect or spreading rays. In *Lysurus Gardneri* there are five rays united at their apices, leaving vertical slits between; in *Lysurus Mokusin* there are also five, primarily apically connected, and then separate, but more or less erect. In *Lysurus aseroëformis* the rays are more numerous, irregularly dichotomous, and in the early stages in vertical apposition; but they subsequently open up and spread out like the petals of a flower (Pl. XV, Figs. 5, 5 *a*, 5 *b*). In *Calathiscus sepia* the margin of the receptacle is expanded and elevated above the hymenium in the form of a cup, with twenty narrow erect cirrhose rays. It is in the genus *Aseroë*, however, that the most striking forms are to be found (Pl. XV, Fig. 6). The rays are generally horizontal, spreading like the tentacles of an anemone, vary from five to twenty in number, and are more or less bifid. The breadth of the stellate disc varies from about 2½ inches in *Aseroë rubra*, Labill., to nearly a foot in *Aseroë Junghuhnii*. The hymenium either forms a ring around the central opening in the disc, or extends some distance on the upper surface of the rays. In eight cases the odour is not given, in the remaining three it is foetid.

In the fourth group are those species in which the receptacle is developed in the form of an ovoid or subglobose lattice, bearing the hymenium in its interior. It may be exceedingly open, as in *Laternea*, in which two (*Laternea pusilla*), three (*Laternea triscapa*), or four (*Laternea columnata*, *Laternea angolensis*) columns are apically united and widely separated; or it may be much closer, passing through such forms as *Colus hirudinosus* (Pl. XV, Fig. 7), in which the lateral columns are increased in number, and at their apices united by a localised and limited mesh-work, to *Clathrus* and *Ileodictyon*, which are subglobular and reticulate (Pl. XV, Fig. 8). Of the 12 species given in the table the receptacle in eight is red (66·6 per cent.), and in four white. The colour of the external peridium is given in 11 cases—in nine it is white, in one brown, and in one darkish. The odour is stated in six cases—in four it is not foetid, and in two foetid.

The general results in regard to colour and odour are summarised in Table III.

TABLE III.

		Colour													Odour of Deliquescing Hymenium.		
		Of Receptacle, or part conspicuous during Deliquescence of Hymenium.				Of External Peridium, which has no relation to the Deliquescence of the Hymenium,							Of Deliquescing Hymenium.				
		White or Whitish.	Red or Reddish.	Yellowish.	Green.	Dark.	White or Whitish.	Reddish.	Brownish.	Purplish.	Yellowish.	Blackish.	Not stated.	Dark.	Orange Red.	Not stated.	Fœtid.	Not Fœtid.	Not stated.
I. Stalked Forms.	A. Without veil or rays	9	11	4			11	1	1		2	1	8	14	1(?)	9	11	1	12
	B. With a veil	10	1			1(?)	5		2				5	5		7	3	1	7
	C. With rays	1	10[1]		1		10			1				9		2	3		8
I. Latticed Forms.		4	8				9		2				1	8		4	2	4	6
	Totals	24	30	4	1	1	35	1	5	1	2	1	14	36	1(?)	22	19	6	33

[1] *Aceroë iridis* sometimes occurs entirely red, and is included here also.

We see from this table that in the Phalloidei the receptacle, or the part that is conspicuous during the exposure of the deliquescing hymenium, is some tint of red in more than half the species, and white in nearly the other half; these two colours occurring in above 91 per cent. of the species. Those with yellow receptacles are confined, with the exception of *Ithyphallus* (*Phallus*) *tenuis*, to the genus *Simblum*, although others may have yellow tints in particular parts, or as varieties (see Table II).

The question now arises whether the colours exhibited by the receptacles of the Phalloidei correspond with the colours of the receptacle in other fungi. I give in Table IV the percentages of the colour of the receptacle in 1288 species of fungi other than Phalloidei as shown in Tulasne's Fungi Hypogaei, in Cooke's[1] plates of the Agarici in his Illustrations of British Fungi, and in Bulliard's Champignons de la France in the Herbier de la France, which comprises fungi of many groups.

TABLE IV.

	Bright Red.	Pure White.	Reddish.	Whitish.	Pure Yellow.	Yellowish.	Green or Bluish.	Purplish.	Browns, Slate, Black, &c.
	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
1. Fungi Hypogaei (44 species)	0·0	4·5	2·2	9·1	0·0	4·4	2·2	2·2	75
2. British Agarici (709 species)	1·5	6·6	3·6	8·6	1·4	3·2	0·7	?	74
3. Champignons de la France (535 species)	5·2	4·6	4·4	5·9	1·4	3·1	3·1	0·9	70·8
Average .	3·0	5·7	3·9	7·5	1·4	3·2	1·7	?	73·1

It is very clear from this table that the coloration of the Phalloidei is exceptional. We see that among them 91·5 per cent. are either red or white, while only 20·1 per cent. of

[1] Nos. 19, 20, 21, 25, 29, 30 were not accessible to me.

other fungi are so coloured; and, further, that while the great majority (73·1 per cent.) of other fungi are of dull tints —browns, slate, blacks, etc.—such colours are not represented among the Phalloidei, with the doubtful exception of *Dictyophora radicata*. And this is not all, for while a large number of those included among other fungi as red or white have impure tints, the great majority of the Phalloidei have colours very brilliant and pure.

I think the inference is evident that the brilliant tints of the Phalloidei have been developed to render them conspicuous.

The utility of a colour in making an object striking or in concealing it of course depends upon the background, and in order to test how the colours of fungi may serve for either of these purposes I made the following experiments. I placed a series of equal-sized, differently coloured discs perpendicularly in the ground in the locality where *Phallus* grows (dark-brown soil with a sprinkling of green herbs, in a wood), and observed the relative effect at various distances, with the following results: (1) Brown, blackish, and purple soon became indistinct and indistinguishable: they served to conceal. (2) Blue was fairly conspicuous near, but not at a distance. (3) Green was conspicuous against the bare soil only. (4) Pale yellow was much more conspicuous than any of the above, and to considerable distances. (5) Red was strikingly conspicuous near, and to considerable distances. (6) White was very conspicuous near, and to the greatest distance of all. A glance at the habitats of the Phalloidei, given in Table II, will show that against such backgrounds red and white and yellow must be very conspicuous. There are two apparent exceptions in the case of *Dictyophora radicatus*. Mont., and *Aseroë viridis*, Berk. The former is described as being all sooty black, and it grows on 'the ground' in Cayenne. If this be the colour of the receptacle while the hymenium is exposed, it forms a striking exception to all other Phalloidei. The case of *Aseroë viridis* is different and very interesting, inasmuch as two varieties are found, one metallic green, growing on 'clay-banks,' and the other of a more or less deep red, growing on the ground, and

presumably among green vegetation. If the clay-banks are almost destitute of green vegetation, and especially if they are whitish or reddish, the green colour of the fungus may serve to make it conspicuous. It is not stated whether it has odour or not.

As is well known from the labours of Sprengel, Darwin, Müller, and others, the colours of flowers have been gradually developed by the beneficial visits of insects, and in Table V the percentage proportions of several colours are given in the case of flowers, Phalloidei, and other fungi.

TABLE V.

	White.	Yellow.	Red.	Blue.	Violet.	Green.	Brown or blackish.
Flowers[1] (4197 species) . . .	28·5	22·6	21·96	14·1	7·3	3·6	0·5
Phalloidei { Receptacle (59 species)	40	6·4	50	0·0	0·0	1·6	1·6 (?)
Phalloidei { Volva (45 species) .	77·2	4·5	2·2	0·0	2·2	0·0	13·5
Other fungi (1288 species) . .	13·2[2]	4·6	6·9[2]		?	1·7[3]	73·1

These figures bring out very strikingly the preponderance of flower-like hues among the Phalloidei in comparison with other fungi; 73 per cent. of flowers, 96·6 per cent. of Phalloidei and only 24·7 per cent. of other fungi being either white, red, or yellow. Blue and violet, which are common enough in flowers, are rare among fungi. The reason of this comparative commonness in the former may be explained by the fact that they are, as a rule, found in highly developed flowers, which are fertilised by the more specialised insects; in other words, that these colours are the result of the effort of the flower not merely to make itself conspicuous, but at the same time to differentiate itself from the commoner colours of the more abundant flowers, so that the insect may discover the par-

[1] Köhler and Schubler, quoted in Balfour's Manual of Botany, p. 329.
[2] Including impure tints. [3] Including bluish.

ticular flower at a glance. This element of complexity in the colour-relations of flowers is absent in the case of the Phalloidei.

It will be observed that the colours of the volva do not correspond with those of the receptacle, but tend rather to approximate to those of ordinary fungi. The preponderance of white may be accounted for by this being the colour of the mycelium, and since the volva is usually subterranean, and therefore not visible during its development, there is no particular call for specialisation; but in some cases it may ultimately serve as an aid in revealing the receptacle, or as a protection by resembling the colour of its surroundings, e.g. *Phallus xylogenus,* Mont., which grows on decaying wood, and has a black peridium. There is another point in these colour-relations worthy of remark. Among flowers the part most exposed is most brightly coloured, and the colour, as a rule, is not fully developed until it is needed, i.e. when the stigma or anthers are mature and the flower is ready to open. The same is precisely the case in the Phalloidei. In *Dictyophora indusiata* (Vent.) the veil which is at first white becomes reddish as the deliquescence proceeds ('en vieillissant'), and this change or deepening of tint also occurs in *Lysurus Mokusin* (Cibot), *Lysurus aseroëformis*, Corda, *Clathrus cancellatus*, etc. Further, the most exposed part is invariably, as in flowers, the part most brilliantly coloured, as may be seen from the description of the stellate and latticed forms in Table II (pp. 222, 223), in which the upper surface of the rays and the outer and upper parts of the lattice are most brightly tinted[1]. It is also to be noted that

[1] The whole question of the function of colour in fungi in relation to their environment is one which has not yet received the attention it deserves. Grant Allen (The Colour-sense, p. 49) suggests their similarity to the 'possibly adventitious colouring of the lower animal forms, such as sea-anemones, star-fish, and medusae.' So far as my studies have gone, colour in fungi serves functionally to act on the colour-sense of animals:—(1) For concealment; hence the predominance of dull tints (Table IV), the upper part of the pileus and the lower and larger portion of the stem being usually similarly coloured and darker, the lower surface of the pileus and the adjacent part of the stem being as a rule paler, i.e. preserving to a greater extent the primary appearance of the mycelium; (2) For con-

the foetid odour is not developed until the change in the consistency of the hymenium allows the spores to be sucked up by the flies.

In regard to odour, in the 25 species in which its presence or absence is mentioned there are 19 (76 per cent.) foetid, and six (25 per cent.) not foetid; while among the flowers of 4,189 species of phanerogams examined by Köhler and Schubler[1] only 417 (9·9 per cent.) had odour. There seems to be no relation between the presence or absence of odour and the degree of conspicuousness; the most inconspicuous (e.g. *Phallus curtus*, Berk.) and the most conspicuous forms (e.g. *Clathrus cancellatus*) may be equally foetid, and *vice versa*. The odour is sometimes most intense. Cooke[2], for instance, says:—'The experience of more than one artist, who has attempted the delineation of *Clathrus* from the life, is to the effect that the odour is unbearable even by an enthusiastic artist determined on making a sketch.'

I have mentioned the flower-like character of colour and the presence of odour, but in many cases there is a third attraction or subsidiary aid to conspicuousness in the peculiar form of the receptacle, which probably exhibits more variety in this than in any other group of fungi. In *Dictyophora*

spicuousness, and this for two purposes: (*a*) to attract insects, as in the Phalloidei: (*b*) to ward off the attacks of animals by advertising the presence of disagreeable or noxious qualities, as in the case of many poisonous fungi, and, as Darwin, Belt, and Wallace have shown, is the case among certain animals, as bitter brightly coloured caterpillars, etc.

In tabulating the colours of different groups I have been struck by the predominance of brilliant colours, especially red and yellow, among the *Pezizae*, which, differing from most of the Agarici, have the hymenial surface freely exposed, as in the Phalloidei, the spores often lying as a layer on the surface, and also among a small group of Agarici, the Amanita, many of which have beautiful tints and agreeable odours, and grow chiefly in places where insects are abundant. In such cases, and also among the Mycena and several small Agarici, it is usually the margins of the gills or lamellae which are most brightly tinted. The presence of hair-like appendages on the stem, etc., is significant from the function of such structures in relation to the floral parts of many Phanerogams, and it is worth while noting that many brightly coloured *Pezizae* have similar structures arranged like 'guards.' This aspect of fungi is well worthy of further study.

[1] Op. cit., p. 330.

[2] Fungi: their Nature, &c., p. 116.

the remarkable reticulated veil around the stem, produced by the excessive development of a small and unimportant membranous layer that exists in *Phallus*, serves materially to reveal its presence. In *Aseroë* and some species of *Lysurus* we have the assumption of the flower-like stellate form (foreshadowed in *Aserophallus* and *Staurophallus*), and it is in this group also that the most brilliant colours occur, the majority (83·3 per cent.) being vivid scarlet or red. Few flowers can compete in conspicuousness with *Aseroë Junghuhnii*, Schlecht., which forms a red star with 16 or 18 rays, and nearly a foot in diameter. The stellate form, which is assumed by so many flowers both much and little specialised, is the form (as I have shown by experiment, and planimeter measurements) which gives the maximum conspicuousness at moderate distances with the least expenditure of material. It is obvious that the lattice form also furnishes an effective and economically conspicuous receptacle.

The facts above given in reference to the form, colour, and odour of the receptacle and hymenium in the Phalloidei point to adaptation for the purpose of attracting insects, and there is direct testimony that insects do visit several of the species besides *Phallus impudicus*.

Cibot, describing *Lysurus Mokusin*, makes the following observations[1] which imply the visits of insects to the hymenial slime. 'Incrementum intra duodecim fere horarum spatium absoluit, perfectusque statim flaccescere incipit, curuatur, in se recumbit et putridinem sentit; attamen hoc illi rarius accidit, quandoquidem Insecta varia eiusdem substantiae auidissima vix terra emergentem fungum plerumque obsident et ante perfectum vegetationis stadium fere totum absumunt.' Curtis, in referring to *Phallus iosmus*, says[2], 'Flies of all descriptions were much attached to this fungus, and, as well as bees (!?) and beetles, seemed very fond of the shining matter which dropped from the pileus'; and the particular fly he describes as living upon it, and which he figures under the name of

[1] Op. cit., p. 373. [2] Loc. cit.

Borborus hamatus, is 'found on windows in houses, in marshy places, and on putrid substances, as dung-heaps, etc.' In regard to *Foetidaria coccinea*, Aug. de Saint-Hilaire, who found it, says [1], 'Cette plante a une odeur extrêmement fétide et est sans cesse couverte des mêmes mouches que l'on a coutume de voir dans le pays sur les cadavres et les végétaux en putréfaction.' Burmeister found the pileus of *Simblum sphaerocephalum*, Schlecht., covered with a dark violet, semi-fluid mass, 'an der die Fliegen eifrig saugen.' With the very doubtful exception of *Phallus iosmus*, all the above named species are foetid [2].

There is also indirect evidence of the action of flies in the fact that *Clathrus cancellatus* has been found in a wood growing close to the dead body of a dog in advanced decomposition [3], and the Italian botanist Pollini found a specimen of the same species growing on a human skull in a tomb [4]. Corda also states [5] that *Phallus impudicus* is common in Zoological Gardens and pheasanteries, where excrements are of course abundant.

In the Phalloidei then it can scarcely be doubted that we have a group of fungi which have undergone great modifications so as to become adapted for the dispersion of their spores by the agency of insects and especially by those which habitually affect putrid substances, and would therefore deposit the spores on the most suitable nidus for their growth. It is an example of the substitution of the more certain action of

[1] Op. cit., tom. iii., p. 192.

[2] I am informed by Professor Bayley Balfour and Dr. J. M. Macfarlane that specimens of *Cynophallus caninus*, which they found in a wood in Ayrshire last summer, were exceedingly attractive to flies, which were 'very like the ordinary house-fly in size and appearance.' In these specimens the stalk was yellow, and the head bright red. *Cynophallus caninus* has been hitherto described as 'scentless,' but Professor Balfour points out that the odour in the above case 'was quite conspicuous, not so strong as that of *Phallus impudicus*, but of the same character.' It is highly probable that further observations on fresh specimens of other species will reduce the number of 'odourless' forms.

[3] Bull. de la Soc. Bot. de France, tom. xx. p. 131. 1873.

[4] Loc. cit. p. 132.

[5] Icon. Fungi, loc. cit.

insects for the uncertain action of the wind, just as in the case of the cross-fertilisation of flowers, where the former agency has so largely replaced the latter. It is easy to understand the utility of this substitution, for if one consider a certain area, as a field or wood, and the proportionately small surface occupied by putrescent matter, it is evident that of the spores blown about at random by the wind the number deposited on such substances will be very small compared with the number lost. If the relative areas be as one to a thousand, on an average 999 spores will be sacrificed for every one deposited; for the agency is, so to speak, rigidly neutral and impartial. In the case of the insects, however, the proportional loss would be very much less, for, guided by their senses, they would tend to pass directly from one seat of putrid matter to another.

Now, since the sole reason of an aërial receptacle in fungi is for the formation and dispersion of the spores, it follows that the Phalloidei must be regarded as exceptionally highly organised; and I will sum up their chief characters that point to this as follows:—

(1) The formation and maturation of the spores within a closed volva, usually subterranean and protected largely from injury.

(2) The sudden emergence and expansion of the receptacle, not by the comparatively slow process of cellular growth, but by a mechanical springlike apparatus acting quickly.

(3) The freely exposed hymenium undergoing rapid mimetic changes, whereby putrid matters are simulated in colour, consistency, and usually odour.

(4) The development of a striking form, and of such colours as will make the receptacle most conspicuous, and the production of accessory parts for the same purpose.

(5) The rapidity of the whole cycle of phenomena by which the risk of accidental destruction, by animals, etc., is lessened, and the effective dispersion of the spores secured.

I may finally add a word as to the importance of these observations that flies and other insects transport living spores of

fungi in relation to the transport of bacteria. The teleology of the bad odours of putrefaction has, so far as I am aware, never been explained; but since these odours depend upon the presence of organisms, and serve to attract multitudes of flies, and since it is a rule in Nature that no organism aids another except, so to speak, with the object of ultimately benefitting itself, it seems to me highly probable that the odour of putrescent matter has been developed in relation to the visits of flies. The advantage to the bacteria is obvious, for by the odour produced, the irregular fortuitous action of the wind is largely replaced by the direct purposive action of insects; and hence, once the odour is developed, flies will form the chief means of dispersal. It has been shown above that spores may retain their vitality during their passage through the digestive canal of flies, and there can be little doubt the same applies to bacteria. Flies may thus serve to disperse not only the micro-organisms associated with putrefaction, but also those which are the cause of certain diseases, such as anthrax, etc., in which the products are attractive to them; and since flies, apart from their own powers of locomotion, are known to be carried long journeys in railway trains and steamers, they may serve to carry infection and spread diseases to distant places.

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EXPLANATION OF FIGURES IN PLATE XV.

Illustrating Dr. T. Wemyss Fulton's paper on Dispersion of Spores of Fungi by the Agency of Insects.

Fig. 1. *Phallus curtus*, Berk. (after Corda).

Fig. 2. *Aserophallus cruciatus*, Lepr. et Mont.

Fig. 3. *Simblum periphragmoides*, Klotsch.

Fig. 4. *Dictyophora speciosa*, Klotsch (reduced ½).

Fig. 5. *Lysurus aseroëformis*, Corda. 5 *a*, 5 *b* showing the progressive expansion of the rays.

Fig. 6. *Aseroë actinobola*, Corda (after Berkeley).

Fig. 7. *Colus hirudinosus*, Cav. et Séch.

Fig. 8. *Clathrus pusillus*, Berkeley.

Fig. 9. *Coprinus deliquescens* (after Bulliard).